

FOSSIL EVIDENCE REGARDING THE EVOLUTION OF *NOTHOFAGUS* BLUME

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ABSTRACT

Information on fossil *Nothofagus*, and related genera, is reviewed based on pollen grains, leaves, woods, and flowers and fruits. The available data suggest that ancestors of *Nothofagus* and related families probably originated in West Gondwanaland. By the Santonian, *Nothofagus* was the only living genus already differentiated in the southern Hemisphere. Northern counterparts included several species in living genera of the Betulaceae, Myricaceae, and Ulmaceae. Rapid evolution and speciation of *Nothofagus* took place in the Eocene. After the pollen types and the main leaf forms were established in the Cretaceous and Eocene, respectively, the rate of morphological change was slow. More speciation was possible after the Miocene in New Guinea and also in other areas during the Plio-Pleistocene. Several lines of evidence support former suggestions of giving *Nothofagus* a higher taxonomic rank.

Nothofagus Blume has frequently captured the interest of botanists and paleobotanists. It plays a dominant role in the temperate forests of the Southern Hemisphere, has economic importance as a timber source, and has an intriguing distribution as a vicariant of the other genera in Fagaceae. It comprises 34 species living in South America, Australia, New Zealand, New Caledonia, and New Guinea. It certainly lived in Antarctica, but perhaps never in South Africa.

The Fagaceae are usually associated with the Betulaceae in the order Fagales (Thorne, 1983; Takhtajan, 1980), sometimes including also the Balanopaceae (Cronquist, 1968). Other related orders are Didymelales, Casuarinales, Myricales, and Hamamelidales, all included in the subclass Hamamelidae. Although this subclass has been subjected to considerable systematic rearrangement (Thorne, 1973), the taxa mentioned above were not very much affected.

The Fagaceae have been segregated into three subfamilies since De Candolle (1864), and this classification has been supported by modern studies such as those of Forman (1966) and Hjelmqvist (1948) on the female cupule. The only objection has been the proposal to segregate *Nothofagus* as a new family, made by Kuprianova (1965), on the basis of the pollen grains. More recent support for some kind of segregation was advanced by Crepet and Daghljan (1980), Smiley and Huggins (1981), Thorne (1983), Nixon (1984), and Jones (1984b). The classification of the species of *Nothofagus* into two sections and four series was suggested by van Steenis (1953)

and Soepadmo (1972) on the basis of the female cupule and vegetative morphology. Recent information does not support fully such an arrangement (Elias, 1971; Philipson & Philipson, 1979; Hill, 1983), but no alternative system has been proposed.

In recent years a growing body of information has accumulated about fossil materials of *Nothofagus* and related genera, shedding some light on its history and phylogenetical development. This information has not been fully used, and speculation about the evolution and paleobiogeography of the genera has been based mainly on the evidence of living plants (van Steenis, 1971; Darlington, 1965; Melville, 1973, 1981; Cracraft, 1975; Humphries, 1981, 1985; Heads, 1985). Therefore, it seems reasonable to review information concerning fossil forms.

Modern and fossil data are reviewed first in this paper, followed by a discussion. The review of fossil data is arranged by type of fossil (pollen, leaves, woods, and flowers and fruits). In each case, a brief statement about their morphology in living plants is given. The discussion starts with the Cretaceous history of the genus, and also deals with the fossil record of related families. Then, the Paleogene account comprises the differentiation of species within the genera, so the morphology of the living ones is also considered. Finally, the Neogene part deals mainly with biogeography, and the information concerns primarily living plants. The fossil evidence was compiled by Wolfe (1973) and Muller (1981). When some information is given without men-

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tioning the source, it may be found in these reviews. However, in important cases the original publication is given. Other more recent papers, or ones not considered by Wolfe or Muller, are quoted as well. The references to paleogeography are based on Smith et al. (1981) and those to age are based on Harland et al. (1982).

DATA

POLLEN GRAINS

Pollen grains of *Nothofagus* are highly characteristic and easily determined. They are small- to medium-sized, peroblate, stephanocolpate, crassimarginate, with a spinulose exine. The living species have been studied in detail by Hanks and Fairbrothers (1976) and Praglowski (1981, 1982). There are three different types ("brassi," "fusca," and "menziesi") differing in the shape of the mesocolpi, and the size and thickening of the colpi. These pollen grains are very different from others in related genera within Fagaceae, or in related families, which are mostly tricolporate, with variable, non-spinose sculpturing.

Fossil pollen grains provide the most complete record of *Nothofagus* through geological time. They appear for the first time in sediments of Santonian age in southern Australia (Dettmann & Playford, 1969; Stover & Evans, 1973) with the "brassi" type. This type was found also in the Campanian of New Zealand (Couper, 1960) and in the Maastrichtian of South America (Archangelsky & Romero, 1973; Romero, 1973). The "fusca" type was present in the Maastrichtian of New Zealand and South America and the Paleocene of Australia (Cooper, 1960; Romero, 1973; Martin, 1981). The "menziesi" type was recorded for the first time in the Maastrichtian of South America, and then in the Paleocene of New Zealand and the Eocene of Australia (Cooper, 1960; Romero, 1973; Martin, 1981). Since their first appearance in the Cretaceous the three types of pollen grains show almost no morphological change.

During the Eocene and Oligocene the participation of *Nothofagus* in pollen assemblages reached its maximum (Romero, 1973, 1977; Martin, 1982). During the Miocene it was generally less frequent but it expanded its area, and is recorded for the first time in New Guinea ("brassi" type; Khan, 1974). There are no records of fossil *Nothofagus* from New Caledonia.

Pollen grains of genera related to *Nothofagus*

are also present relatively early. "Celtis type" pollen and "intermediates to *Ulmus* type," as defined by Muller (1981) were described from the Turonian (ca. 90 Ma) of Borneo. Borneo was located close to or at the Equator at that time. Pollen grains of *Alnus*, *Betula*, and *Myrica* were found in the Santonian of Japan, Canada, and the United States, respectively (see Muller, 1981 for references in this paragraph). In the Campanian *Cercidiphyllites* is recorded in Canada, *Momipites* (Juglandaceae) in the United States, and *Castanea* in Canada and Holland. The last one is the first genus of Fagaceae recorded in Laurasia, about 15 Ma, later than the occurrence of *Nothofagus* in Gondwanaland. In the Maastrichtian, the "Ulmus type" was described in Canada, the United States, Brazil, and India. In the Paleocene the "Liquidambar type" (Hamamelidaceae), *Tricolporopollenites parmularius* (Eucommiaceae), and *Carpinuspollenites* (Betulaceae) are all known from central Europe. More importantly two other families of the subclass Hamamelidae with a Gondwanaland distribution appear for the first time during the Paleocene. They are Casuarinaceae, represented by *Haloragacidites* in the Paleocene of New Zealand, Australia, Argentina, and sediments in the Indian Ocean, and Didymelaceae, represented by *Schizocolpus marlinensis* in New Zealand and sediments of the Indian Ocean.

LEAVES

Leaves of living species of *Nothofagus* are rather variable. Those of extant South American, Australian, and New Zealand species (Romero, 1980; Carrasco Aguirre & Romero, 1982) are persistent or deciduous, craspedrodromous (with one exception), and with well marked, sometimes composite teeth. Those of New Guinea and New Caledonia (Romero & Carrasco Aguirre, 1982) are persistent, brochidodromous or semi-craspedrodromous, entire margined or with small teeth. The small teeth are different from those in the former species and were probably independently derived. Leaves of living species of *Fagus* can be differentiated from *Nothofagus* (Jones, 1984a; Dibern & Romero, 1984; Romero & Dibern, 1985) and the same is true for other genera of Fagaceae and related families (Wolfe, 1973). Cuticles of the South American species were studied by Ragonese (1981) while Jones (1984a) also sampled several species from Aus-

tralia, New Zealand, New Guinea, and New Caledonia.

Imprints of leaves of indubitable *Nothofagus* fossil species are not present until the Eocene, and they are probably more frequent during the Oligocene (Ettingshausen, 1886, 1888; Dusen, 1907, 1916; Romero, 1978; Holden, 1983; Hill, 1983). Several show strong similarities with living species, and thus indicate a very low rate of morphological change (Dibbern & Romero, 1984).

Species of *Ulmus*, *Betula*, and *Alnus* were also described in the Southern Hemisphere (Ettingshausen, 1886, 1888; Dusen, 1907, 1916) and they will probably prove to be *Nothofagus*. However, it is noteworthy that a revision (Romero & Dibbern, 1985) of the original types of Dusen showed that some South American fossils described as *Fagus* could not be classified among living *Nothofagus* and fall within the limits of variation of *Fagus*.

Upper Cretaceous and Paleogene sediments both in the Gondwanaland and Laurasian continents also yielded some extinct genera of supposed Fagaceae, such as *Debeya*, *Dryophyllum*, *Fagophyllum*, and *Fagopsis* (Ettingshausen, 1886, 1888; Dusen, 1916; Berry, 1937). However, the delimitation and definition of these genera was done also many years ago in the Northern Hemisphere, and was based only on gross morphology. Its use, especially in Gondwanaland, should be revised in the light of modern concepts of leaf architecture. The studies of Manchester and Crane (1983) and Jones (1984a) show the trend to be followed.

Among related families, important records of fossil leaves are those of *Alnus* from the Maastriichtian of British Columbia; *Corylopsis*, *Corylus*, and *Sinowilsonia* from the Paleocene; and *Carya* and *Tetracentron* from the Eocene, from several localities in the United States (see references in Wolfe, 1973).

Without familial or ordinal assignment, the earliest fossil leaves considered "to be members of a trend" to the subclass Hamamelidiae are some "Platanoids" from the Albian of the Potomac Group, eastern United States (Hickey & Doyle, 1977; Doyle & Hickey, 1976). Another early leaf that shared some Hamamelidoid and Magnolioid characters is an unnamed one, from the Baqueró Formation in Patagonia, Argentina and is late Barremian to early Aptian in age (Romero & Archangelsky, 1985).

Cuticles of fossil *Nothofagus* have been studied

in a few Eocene and Oligocene species by Hill (1983) and Jones (1984a).

WOODS

Nothofagus timber has commercial value and its anatomy has been well known for many years (Dadswell & Eckersley, 1935; Dadswell & Ingle, 1954; Hinds & Reid, 1957; Tortorelli, 1956; Wagemann, 1948). Practical keys for use in each country were published, allowing identification of every species.

Fossil woods of *Nothofagus* have been described from strata of different ages in South America. The oldest is *Nothofagoxylon pichasquensis* (Torres & Rallo, 1981) from the Upper Cretaceous of northern Chile. It is associated with dinosaurs and turtles, at about 25°S of paleolatitude. Seven other species were found in Eocene, Oligocene, or undifferentiated Tertiary rocks (see review in Ragonese, 1977; and Torres, 1984). In Oligocene (?) sediments of Río Turbio, southernmost Argentina, Salard (1961) described a species of *Fagoxylon*.

A doubtful *Nothofagoxylon* was studied from New Zealand (Evans, 1931). As far as I am aware, there are no other woods described as *Nothofagus* in recent times. Among related families, there is an important record of woods of Platanaceae in the Campanian of the United States, which is the first record of woods of the subclass (Wolfe, 1973).

FLOWERS AND FRUITS

The cupule of *Nothofagus* is interpreted as a reduced dichasium (Forman, 1966). Its relationships with other genera have been established by Forman (1966) and Endress (1977). One of the species (*N. alessandri*) has retained seven flowers, which is probably the most primitive number of flowers in the family. *Nothofagus nitida* occasionally has five (van Steenis 1953: 312).

The only flower reported from the Southern Hemisphere is a four-parted cupule from the Oligocene of Tasmania (Hill, 1983) whose affinities to living species could not be established. In the Northern Hemisphere several flowers were attributed to Fagaceae and related families (Crepet, 1981; Smiley & Huggins, 1981). *Fagopsis*, from Eocene and Oligocene beds in the United States, is especially important (Manchester & Crane, 1983). It is a representative of the Fagaceae, but it is not readily accommodated in any recent subfamily. It has some features similar to every genus in the family, except *Nothofagus*.

DISCUSSION: A PHYLOGENETIC AND
PALEOGEOGRAPHICAL MODEL

On the basis of the preceding data, a scenario may be constructed for the history of *Nothofagus* and related taxa through geological time. The current paradigm for the origin of the angiosperms is that they derived from unknown gymnosperms some place in West Gondwanaland towards the end of the Early Cretaceous (Raven & Axelrod, 1974; Brenner, 1976; Doyle & Hickey, 1976; Schuster, 1976). The subclass Hamamelidae would differentiate in the Northern Hemisphere. Raven and Axelrod (1974) stated that families like Hamamelidaceae, Fagaceae, and Betulaceae would have originated in Laurasia, and particularly *Nothofagus* migrated from Asia through Gondwanaland, via the mountain heights of Africa and India, in the Middle Cretaceous. Wolfe (1973) also believed that most of the Hamamelidae originated in the *Aquilapollenites* province (western North America and Asia) in the Late Cretaceous, and that families such as Fagaceae and Betulaceae evolved there prior to the Maastrichtian, diversifying into extant genera during the Maastrichtian and Paleocene.

The fossil record does not fully support these ideas. As mentioned in the previous chapter, there are leaves of Aptian–Albian age with Hamamelidoid features in relatively high latitudes of both hemispheres. The oldest fossil record determined to family are pollen grains of Ulmaceae of Turonian age in the equatorial belt, in Borneo. And the oldest determined to genus are pollen grains of Santonian age, also at high latitudes in both hemispheres: *Nothofagus* in Australia and *Alnus*, *Betula*, and *Myrica* in Japan, Canada, and the United States. Therefore, it seems more plausible that the subclass originated in tropical areas of West Gondwanaland, with different families differentiating polewards. *Nothofagus* was at that time the only representative of Fagaceae being a vicariant of the northern Betulaceae and Myricaceae. Such an early differentiation of only this genus from related families would support the above mentioned suggestion to segregate Nothofagaceae as an independent family.

From West Gondwanaland, the ancestors of *Nothofagus* should have migrated to southern South America and/or southern Africa. South America was at that time united to west Antarctica, which in turn was very close to or at the South Pole. Southern Africa was separated from east Antarctica, but only by about 1,000 km; the

coast of east Antarctica was probably at about 60°S. From west or east Antarctica the ancestors of *Nothofagus* should have reached Australia before the Santonian and New Zealand before the Campanian.

Campanian and Maastrichtian times witnessed the diversification and migration of *Nothofagus*, which occupies every Gondwanaland land mass, except South Africa and India, and is recorded with the three types of pollen grains and petrified trunks. In the Laurasian continents, in contrast, there is a radiation of different families: Platanaceae, Cercidiphyllaceae, Juglandaceae, and Fagaceae (Castaneoideae), which may be found in widespread outcrops as different kinds of fossils.

By the Paleocene and Early Eocene, *Nothofagus* was represented in the Southern Hemisphere, though it was still not dominant. Casuarinaceae and Didymelaceae, the two other southern families of the subclass, are recorded for the first time. Also there are some cosmopolitan genera (*Dryophyllum*, *Fagophyllum*) usually, yet with growing hesitation, attributed to the Fagaceae. In any event, there is evidence for a relatively important hamamelidaceous genetic stock in the Southern Hemisphere. In the Northern Hemisphere the radiation continued, with records of the new families Eucommiaceae and Hamamelidaceae, and more genera in the Platanaceae, Betulaceae, Ulmaceae, and Juglandaceae. The Fagaceae were still only represented by the Castaneoideae.

During the Eocene the Fagaceae had a rich fossil record comprised of every kind of fossil. In South America, *Nothofagus* is represented by abundant woods, leaf imprints, and pollen grains, and may be dominant in the floras. Australian authors (Christophel, 1981; Martin, 1981, 1982) remarked that in Australia pollen grains of *Nothofagus* may be very abundant in Eocene sediments, but imprints of leaves are very rare, if even present. This is explained by a mosaic pattern of forests with patches of a subordinate *Nothofagus*, but with favorable conditions for dispersal of the pollen grains.

Fagaceous leaves of Eocene deposits are the oldest that can be placed in extinct species of living genera. They belong to *Quercus*, "*Castanea*," and *Fagus* in the Northern Hemisphere and to *Nothofagus* in the Southern Hemisphere.

As noticed above, very low rates of morphological change in *Nothofagus* are recorded in their pollen grains since the Cretaceous and in their

leaves since the Eocene. These long periods of stasis seem to conform to the "punctuated equilibrium" model of evolution. However, the process and timing of the radiation of the stable species in both cases is not well established.

Most of the South American fossil leaves that resemble those of living species are similar to the deciduous taxa inhabiting the northern part of *Nothofagus* distribution, in northwest Patagonia (Romero & Dibern, 1985). Also I restudied fossil leaves from Australia, formerly published by Ettingshausen (1888) and found that deciduous species were present there at the same time. Therefore, there is a strong possibility that we are witnessing in these floras the development of deciduousness in *Nothofagus*, or at least an adaptive radiation from deciduous ancestors in Antarctica. About 35 to 40 Ma, that is, by Late Eocene or Early Oligocene, Australia was separated from Antarctica (Raven & Axelrod, 1972; Kemp, 1978). A more continuous oceanic current developed around Antarctica, substantially changing the climate of the Southern Hemisphere. The development of deciduousness was a probable response to that change (Romero, 1984). Later, in connection with the migration of Australasia to the north (Kemp, 1978; Martin, 1981; Smith et al., 1981), some extinction occurred there leaving the Tasmanian *N. gunni* as the only deciduous species.

Leaf taphofloras and palynofloras of Eocene and Oligocene age show repeatedly a mixture of species of supposed cold temperate climate with others of supposed subtropical or tropical climate (Kemp, 1978; Romero, 1978, 1984). They are rather variable through geological time and latitude, and have different percentages of *Nothofagus* as the most important cold temperate element. The same authors suggested that these Paleogene associations are not represented by any of the living plant associations.

A problem is imposed by the presence in South America of fossils attributed to Fagaceae, which are beyond the range of variation of *Nothofagus* and within that of *Fagus*. They are leaves and woods and were reported as southern *Fagus*. Similar but more doubtful remains were described from Australia and New Zealand. A genetical relationship with *Fagus* seems unlikely, and it is more reasonable to expect some kind of convergence between taxa belonging to the same genetic stock (no matter if it is considered at the familial, ordinal, or superordinal level) and that have remained isolated since the Creta-

ceous. A similar and consistent case for convergence could also be made for supposed *Nothofagus* widespread in North America (Elsik, 1974). They are not really *Nothofagus* (Romero, 1977: 181; Muller, 1981) but share important characters.

The oldest records of pollen grains of *Quercus* and *Fagus* are from the Oligocene, several million years after the first record of leaves (Romero, 1984). This contrasts with the long history of the pollen grains of *Nothofagus* and supports the consideration of the southern genus as a more independent, earlier derived taxon. Also, the Oligocene record of *Fagopsis* in the United States, showing features of different genera of Fagaceae, except *Nothofagus*, is additional argument for an independent treatment of this genus.

During Late Eocene and Oligocene times, New Guinea rose above sea level (Axelrod & Raven, 1982). The earlier records of *Nothofagus* are pollen grains of Miocene age. Raven and Axelrod (1972) suggested that the genus migrated from northwest Australia and then diversified during the Pleistocene. New Caledonia has remained isolated since the Cretaceous, and has no fossil record. Raven and Axelrod (1972) believed that the *Nothofagus* species also remained isolated and are remnants of the old Antarctic stock. Therefore, according to these authors, New Guinea and New Caledonia received different contingents of species, from different continents and with a gap of about 50 million years. However, the living plants in both archipelagos are extremely similar in their flowers (Soepadmo, 1972), leaves (Romero & Carrasco Aguirre, 1982), pollen grains (Cookson & Pike, 1955), wood (Dadswell & Ingle, 1954), and ecology (Ash, 1982). The botanical evidence seems to indicate that the migration occurred from one of the archipelagos to the other, but it is not clear which one was the source and when it happened.

The Pliocene and Pleistocene were times of important climatic changes, related to glaciation and fluctuations of sea level. They produced extinctions in some groups of plants and diversification in others. Extinctions occurred with the species producing pollen of the "brassi" type in South America, New Zealand, and Australia. Radiation occurred in New Guinea, where the uplift of the mountains favored the differentiation of 13 still closely related species.

There are also other groups of species very similar morphologically, which probably differentiated very recently. One group is that of *N.*

betuloides, *N. dombeyi*, and *N. nitida*, with similar flowers (van Steenis, 1953), leaves (Romero, 1980), cuticles (Ragonese, 1981), and pollen (Heusser, 1971; Markgraf & D'Antoni, 1978), which may produce hybrids in mixed populations (Donoso & Atienza, 1984). Another group of this kind, in New Zealand, is that formed by *N. fusca* and *N. truncata*, which have the same similarities and frequently hybridize (Cockayne & Atkinson, 1926). Finally, *N. antarctica* has marked ecotypes, and *N. solandri* has subspecies, which are evidences of very recent pressure of selection towards speciation.

CONCLUSIONS

The fossil record supports several plausible hypotheses regarding the evolution of *Nothofagus* and related taxa. They are:

1) Ancestors of Hamamelidales and related orders differentiated in tropical areas, in West Gondwanaland. By the Santonian they had migrated toward Laurasia, where Ulmaceae, Betulaceae, and Myricaceae radiated, and towards southern Gondwanaland, where only *Nothofagus* ancestors evolved. This would support the suggestion of giving a higher rank to the southern genus.

2) *Nothofagus* ancestors migrated from tropical West Gondwanaland to southern South America—west Antarctica, and/or to southern Africa—east Antarctica. From Antarctica they reached Australia in the Santonian and New Zealand in the Campanian.

3) During the Eocene living genera of Fagaceae differentiated in the Northern Hemisphere and direct ancestors of living species of *Nothofagus* differentiated in the Southern Hemisphere. These changes are registered by fossil leaves that represent the onset of deciduousness in response to global climatic changes. Deciduous species of *Nothofagus* were present in Australia and New Zealand, but were subsequently lost.

4) Long periods of stasis in the morphological change of fossil species seem consistent with the punctuated equilibrium model, but the early, rapid differentiation of the group is not yet well documented.

5) During Eocene times, *Nothofagus* was a member of mixed forests, comprised of subtropical and temperate elements.

6) *Nothofagus* reached New Guinea by Oligocene or Miocene times. The circumstances of migration to New Caledonia are not clear. Bo-

tanical evidence is consistent with exchanges between the two archipelagos.

7) Climatic changes during the Pliocene and Pleistocene were responsible for the extinction of the *Nothofagus* "brassi" group in Australia, New Zealand, and South America, as well as for speciation between several closely related modern species.

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